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NONLINEAR DYNAMICS OF MULTI-CHANNEL BINOCULAR VISION

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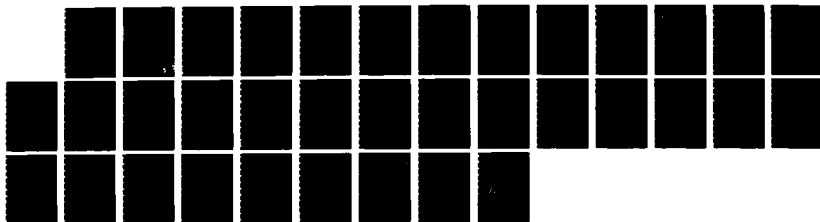
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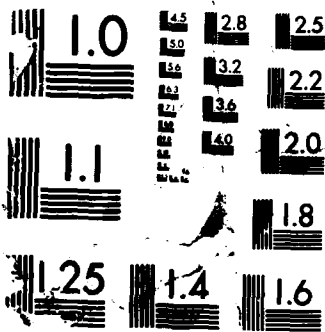
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During the three-year funding cycle, our group has made major progress in several important areas of psychology and neurobiology. In every area, we have discovered new principles of behavioral organization, have translated these principles into real-time adaptive neural networks, have used these models to unify the explanation of large interdisciplinary data base through systematic computer simulations and mathematical analyses, and have thereby characterized these circuits for implementation as new types of parallel computers in artificial intelligence applications.

A large number of new predictions have also been made. Several of them have received experimental support during the funding cycle. A number of older predictions have also received experimental support during the funding cycle. In addition to our modelling work, several articles reporting experimental results on surface perception (shape-from-shading) have also been prepared and published.

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**FINAL SCIENTIFIC REPORT**

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**NONLINEAR DYNAMICS OF MULTI-CHANNEL BINOCULAR VISION**

**Principal Investigator: Stephen Grossberg**  
**Professor of Mathematics, Psychology, and Biomedical Engineering**  
**Director, Center for Adaptive Systems**  
**Boston University**  
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*syndes: psychology, neurobiology, color vision*

## PART I

### BOOKS AND ARTICLES PREPARED WITH AFOSR SUPPORT

January 15, 1982--January 31, 1985

#### Books

- +\*1. Grossberg, S., **Neural Models in Psychology: The Grossberg Lectures**. P. Killeen and D. Hestenes (Eds.). Hillsdale, NJ: Erlbaum, 1985, in preparation.
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*Performance*, 1984, 10, 740-745.

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## PART II

### REVIEW OF RESEARCH

#### 1. Introduction

During the three-year funding cycle, our group has made major progress in several important areas of psychology and neurobiology. In every area, we have discovered new principles of behavioral organization, have translated these principles into real-time adaptive neural networks, have used these models to unify the explanation of large interdisciplinary data bases through systematic computer simulations and mathematical analyses, and have thereby characterized these circuits for implementation as new types of parallel computers in artificial intelligence applications.

A large number of new predictions have also been made. Several of them have received experimental support during the funding cycle. A number of older predictions have also received experimental support during the funding cycle. In addition to our modelling work, several articles reporting experimental results on surface perception (shape-from-shading) have also been prepared and published.

Due to the extent and interdisciplinary nature of the results, the following review will describe highlights of each activity. Abstracts of illustrative articles are also included to provide further details.

## **2. Perceptual Dynamics of Form, Color, Lightness, and Depth Perception**

Articles: 7, 8, 9, 10, 15, 16, 17, 18, 20, 23, 25, 26.

In this work, we have been developing a unified theory of how the visual system synthesizes coherent percepts from noisy retinal data. Our work has led us to discover and characterize the processing rules of several interacting visual subsystems: a Boundary Contour System, a Feature Contour System, and an Object Recognition System. The results clarify why alternative approaches have not been able to provide unified explanations of a broad range of visual and neural data.

In particular, many artificial intelligence models for computer vision are based upon 19th century mathematical ideas, such as Laplacian, surface normal, and curvature. All of these concepts describe local properties of geometrical objects. Our results have led to a new understanding of how visual system interactions exploit contextual information, rather than relying upon local data. These results embody new ideas concerning the foundations of geometry, statistical mechanics, decision theory, the resolution of uncertainty in quantum measurement systems, and phase transitions in very large dissipative systems of nonlinear differential equations. Our results hereby suggest a new foundation for theoretical visual studies, and provide converging evidence that such mechanisms are realized in striate and prestriate visual cortex. In addition, we have proved global mathematical theorems to establish the absolute stability of the neural networks which realize our perceptual processing ideas.

Abstracts of several illustrative articles are listed below.

# The quantized geometry of visual space: The coherent computation of depth, form, and lightness

**Stephen Grossberg**

*Center for Adaptive Systems, Department of Mathematics, Boston University, Boston, Mass. 02215*

**Abstract:** A theory is presented of how global visual interactions between depth, length, lightness, and form percepts can occur. The theory suggests how quantized activity patterns which reflect these visual properties can coherently fill-in, or complete, visually ambiguous regions starting with visually informative data features. Phenomena such as the Cornsweet and Craik-O'Brien effects, phantoms and subjective contours, binocular brightness summation, the equidistance tendency, Emmert's law, allelotropia, multiple spatial frequency scaling and edge detection, figure-ground completion, coexistence of depth and binocular rivalry, reflectance rivalry, Fechner's paradox, decrease of threshold contrast with increased number of cycles in a grating pattern, hysteresis, adaptation level tuning, Weber law modulation, shift of sensitivity with background luminance, and the finite capacity of visual short term memory are discussed in terms of a small set of concepts and mechanisms. Limitations of alternative visual theories which depend upon Fourier analysis, Laplacians, zero-crossings, and cooperative depth planes are described. Relationships between monocular and binocular processing of the same visual patterns are noted, and a shift in emphasis from edge and disparity computations toward the characterization of resonant activity-scaling correlations across multiple spatial scales is recommended. This recommendation follows from the theory's distinction between the concept of a structural spatial scale, which is determined by local receptive field properties, and a functional spatial scale, which is defined by the interaction between global properties of a visual scene and the network as a whole. Functional spatial scales, but not structural spatial scales, embody the quantization of network activity that reflects a scene's global visual representation. A functional scale is generated by a filling-in resonant exchange, or FIRE, which can be ignited by an exchange of feedback signals among the binocular cells where monocular patterns are binocularly matched.

**Keywords:** binocular vision; brightness perception; figure-ground; feature extraction; form perception; neural network; nonlinear resonance; receptive field; short-term memory; spatial scales; visual completion

## Neural dynamics of brightness perception: Features, boundaries, diffusion, and resonance

MICHAEL A. COHEN and STEPHEN GROSSBERG  
*Boston University, Boston, Massachusetts*

A real-time visual processing theory is used to unify the explanation of monocular and binocular brightness data. This theory describes adaptive processes which overcome limitations of the visual uptake process to synthesize informative visual representations of the external world. The brightness data include versions of the Craik-O'Brien-Cornsweet effect and its exceptions, Bergström's demonstrations comparing the brightnesses of smoothly modulated and step-like luminance profiles, Hamada's demonstrations of nonclassical differences between the perception of luminance decrements and increments, Fechner's paradox, binocular brightness averaging, binocular brightness summation, binocular rivalry, and fading of stabilized images and ganzfelds. Familiar concepts such as spatial frequency analysis, Mach bands, and edge contrast are relevant but insufficient to explain the totality of these data. Two parallel contour-sensitive processes interact to generate the theory's brightness, color, and form explanations. A boundary-contour process is sensitive to the orientation and amount of contrast but not to the direction of contrast in scenic edges. It generates contours that form the boundaries of monocular perceptual domains. The spatial patterning of these contours is sensitive to the global configuration of scenic elements. A feature-contour process is insensitive to the orientation of contrast, but is sensitive to both the amount of contrast and to the direction of contrast in scenic edges. It triggers a diffusive filling-in reaction of featural quality within perceptual domains whose boundaries are dynamically defined by boundary contours. The boundary-contour system is hypothesized to include the hypercolumns in visual striate cortex. The feature-contour system is hypothesized to include the blobs in visual striate cortex. These preprocessed monocular activity patterns enter consciousness in the theory via a process of resonant binocular matching that is capable of selectively lifting whole monocular patterns into a binocular representation of form-and-color-in-depth. This binocular process is hypothesized to occur in area V4 of the visual prestriate cortex.

## Neural Dynamics of Form Perception: Boundary Completion, Illusory Figures, and Neon Color Spreading

Stephen Grossberg and Ennio Mingolla  
Center for Adaptive Systems, Boston University

A real-time visual processing theory is used to analyze real and illusory contour formation, contour and brightness interactions, neon color spreading, complementary color induction, and filling-in of discounted illuminants and scotomas. The theory also physically interprets and generalizes Land's retinex theory. These phenomena are traced to adaptive processes that overcome limitations of visual uptake to synthesize informative visual representations of the external world. Two parallel contour sensitive processes interact to generate the theory's brightness, color, and form estimates. A *boundary contour* process is sensitive to orientation and amount of contrast but not to direction of contrast in scenic edges. It synthesizes boundaries sensitive to the global configuration of scenic elements. A *feature contour* process is insensitive to orientation but sensitive to both amount of contrast and to direction of contrast in scenic edges. It triggers a diffusive filling-in of featural quality within perceptual domains whose boundaries are determined by completed boundary contours. The boundary contour process is hypothesized to include cortical interactions initiated by hypercolumns in Area 17 of the visual cortex. The feature contour process is hypothesized to include cortical interactions initiated by the cytochrome oxydase staining blobs in Area 17. Relevant data from striate and prestriate visual cortex, including data that support two predictions, are reviewed. Implications for other perceptual theories and axioms of geometry are discussed.

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# Absolute Stability of Global Pattern Formation and Parallel Memory Storage by Competitive Neural Networks

MICHAEL A. COHEN AND STEPHEN GROSSBERG

**Abstract**—The process whereby input patterns are transformed and stored by competitive cellular networks is considered. This process arises in such diverse subjects as the short-term storage of visual or language patterns by neural networks, pattern formation due to the firing of morphogenetic gradients in developmental biology, control of choice behavior during macromolecular evolution, and the design of stable context-sensitive parallel processors. In addition to systems capable of approaching one of perhaps infinitely many equilibrium points in response to arbitrary input patterns and initial data, one finds in these subjects a wide variety of other behaviors, notably traveling waves, standing waves, resonance, and chaos. The question of what general dynamical constraints cause global approach to equilibria rather than large amplitude waves is therefore of considerable interest. In another terminology, this is the question of whether global pattern formation occurs. A related question is whether the global pattern formation property persists when system parameters slowly change in an unpredictable fashion due to self-organization (development, learning). This is the question of absolute stability of global pattern formation. It is shown that many model systems which exhibit the absolute stability property can be written in the form

$$\frac{dx_i}{dt} = a_i(x_i) \left[ b_i(x_i) - \sum_{k=1}^n c_{ik} d_k(x_k) \right] \quad (1)$$

$i = 1, 2, \dots, n$ , where the matrix  $C = \|c_{ik}\|$  is symmetric and the system as a whole is competitive. Under these circumstances, this system defines a

global Liapunov function. The absolute stability of systems with infinite but totally disconnected sets of equilibrium points can then be studied using the LaSalle invariance principle, the theory of several complex variables, and Sard's theorem. The symmetry of matrix  $C$  is important since competitive systems of the form (1) exist wherein  $C$  is arbitrarily close to a symmetric matrix but almost all trajectories persistently oscillate, as in the voting paradox. Slowing down the competitive feedback without violating symmetry, as in the systems

$$\begin{aligned} \frac{dx_i}{dt} &= a_i(x_i) \left[ b_i(x_i) - \sum_{k=1}^n c_{ik} d_k(x_k) \right] \\ \frac{dv_i}{dt} &= e_i(x_i) [f_i(x_i) - v_i], \end{aligned}$$

also enables sustained oscillations to occur. Our results thus show that the use of fast symmetric competitive feedback is a robust design constraint for guaranteeing absolute stability of global pattern formation.

### **3. Experiments on Surface Perception (Shape-from-Shading)**

Articles: 28-32.

These experiments have developed computer graphics programs whereby idealized 2-D images of 3-D surfaces can be constructed and manipulated at will. Using these images, psychophysical methods have been developed to test subjects' percepts of 3-D surfaces. These experimental results have cast serious doubt upon the psychological validity of traditional shape-from-shading algorithms, and have provided essential new data for building an adequate theory of surface perception. An illustrative Abstract is included below.



## **Perception of Surface Curvature and Direction of Illumination From Patterns of Shading**

**James T. Todd**  
Brandeis University

**Ennio Mingolla**  
University of Connecticut

Three experiments examine the perceptual salience of shading information for the visual specification of three-dimensional form. The observers in these experiments were required to estimate the surface curvature and direction of illumination depicted in computer-synthesized images of cylindrical surfaces, both with and without texture. The results indicate that the shininess of a surface enhances the perception of curvature, but has no effect on perceived direction of illumination; and that shading is generally less effective than texture for depicting surfaces in three dimensions. These and other findings are used to evaluate the psychological validity of several mathematical analyses of shading information that have recently been proposed in the literature.

#### **4. Neural Dynamics of Adaptive Sensory-Motor Control: Ballistic Eye Movements**

**Book: 4.**

This book introduces and develops a quantitative neural theory of a complex sensory-motor system: the saccadic eye movement system. Saccadic eye movements are ballistic movements of great speed and accuracy in humans and many other mammals. The present work describes a number of general functional problems which need to be solved by the saccadic eye movement system, as well as by other sensory-motor systems. Specialized neural circuit solutions of these problems, within the context of ballistic eye movements, are used to unify the discussion of a large behavioral and neural data base concerning this sensory-motor system. A substantial number of new experimental predictions are also made with which to further test the theory.

Many of the functional problems for which we have suggested solutions were identified through a consideration of how the saccadic system can automatically calibrate itself through processes of development and learning. We suggest that an analysis of sensory-motor performance, in the absence of an analysis of self-calibration through learning, does not provide enough constraints to characterize the mechanisms of an entire sensory-motor system.

In addition to unifying and predicting data, the present work suggests new real-time circuit designs for adaptive robots, and thus represents a contribution to artificial intelligence, adaptive control theory, and engineering. All of the neural circuit designs are expressed and analysed using the language of nonlinear systems of differential equations. The work is thus a contribution to applied mathematics and dynamical systems. The interdisciplinary nature of the book may make it useful to scientists in several different fields.

Using these results, one can now begin to analyse how mechanisms of visual perception

and of saccadic eye movements work together to build self-consistent representations of rapidly scanned complex scenes.

The scope of this work is illustrated by the book's Table of Contents:

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## 5. Self-Organizing Recognition Processes for Vision, Speech, and Cognition

Articles: 6, 11, 12, 19, 27.

This work has been developing Grossberg's *adaptive resonance theory*. This theory has emerged from an analysis of how recognition codes can be learned, without a teacher, in response to a temporal stream of input patterns. Unlike other theories, our results show how such a self-organizing recognition code can self-stabilize its learning in response to arbitrarily many input patterns of arbitrary complexity. This fundamental insight has enabled the theory to discover and implement a wealth of new ideas about attention, bottom-up adaptive filtering, top-down expectancy learning, pattern matching, habituation of the orienting response, and self-regulating parallel memory search. The results have also led to the introduction of new computational units for use in visual, speech, and language coding, including a new circuit design—called a *masking field*—for rapidly coding multiple groupings of an input pattern.

The models have been tested, for example, by explaining reaction time and error rate data in lexical decision, word familiarity, and word superiority experiments; by analysing and predicting interactions between several evoked potentials (processing negativity, mismatch negativity, early positive wave, P300, CNV); and by providing a rigorous theory in which the intuitions of the major psychological information processing concepts have been modified and thereby unified: e.g., controlled vs. automatic processing, automatic spreading activation vs. conscious attention, letter nodes vs. word nodes in interactive activation models. In every case, deficiencies of earlier models could be traced to their insufficient analysis of relationships between learning and information processing. All the models have a neurophysiological, anatomical, and neuropharmacological interpretation which has received increasing support from recent data.

## **6. Neural Dynamics of Conditioning, Reinforcement, and Attention**

Articles: 13, 14, 19, 21, 22.

These articles have developed a neural theory aimed at explaining a large body of interdisciplinary data about Pavlovian and instrumental conditioning. To accomplish this, the theory has discovered and joined together mechanisms of conditioning, reinforcement, motivation, internal drive (homeostasis), nonspecific arousal, attention, and cognitive processing (Section 5). Such results begin to show how a living system's internal requirements interact with its processing of external events to generate predictively appropriate and efficient motor commands. The results clarify data about interactions between neocortex, hippocampus, hypothalamus, septum, reticular formation, and cerebellum.

From the viewpoint of advanced technology, each of the contributions in Sections 3-6 helps to characterize a different command module that will be useful for designing the freely moving, self-teaching, self-repairing robots of the future.

Two Abstracts and one Table of Contents are listed below to illustrate the scope of the results.

## Processing of Expected and Unexpected Events During Conditioning and Attention: A Psychophysiological Theory

Stephen Grossberg

Department of Mathematics, Boston University

Some recent formal models of Pavlovian and instrumental conditioning contain internal paradoxes that restrict their predictive power. These paradoxes can be traced to an inadequate formulation of how mechanisms of short-term memory and long-term memory work together to control the shifting balance between the processing of expected and unexpected events. Once this formulation is strengthened, a unified processing framework is suggested wherein attentional and orienting subsystems coexist in a complementary relationship that controls the adaptive self-organization of internal representations in response to expected and unexpected events. In this framework, conditioning and attentional constructs can be more directly validated by interdisciplinary paradigms in which seemingly disparate phenomena can be shown to share similar physiological and pharmacological mechanisms. A model of cholinergic-catecholaminergic interactions suggests how drive, reinforcer, and arousal inputs regulate motivational baseline, hysteresis, and rebound, with the hippocampus as a final common path. Extinction, conditioned emotional responses, conditioned avoidance responses, secondary conditioning, and inverted U effects also occur. A similar design in sensory and cognitive representations suggests how short-term memory reset and attentional resonance occur and are related to evoked potentials such as N200, P300, and contingent negative variation (CNV). Competitive feedback properties such as pattern matching, contrast enhancement, and normalization of short-term memory patterns make possible the hypothesis testing procedures that search for and define new internal representations in response to unexpected events. Long-term memory traces regulate adaptive filtering, expectancy learning, conditioned reinforcer learning, incentive motivational learning, and habit learning. When these mechanisms act together, conditioning phenomena such as overshadowing, unblocking, latent inhibition, overexpectation, and behavioral contrast emerge.

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## **A PSYCHOPHYSIOLOGICAL THEORY OF REINFORCEMENT, DRIVE, MOTIVATION AND ATTENTION**

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(Received February 16, 1982)

### **Abstract**

This article derives a real-time theory of motivated behavior and presents some of its physiological and pharmacological correlates. The theory mechanistically explicates instrumental concepts such as reinforcement, drive, incentive motivation, and habit, and describes their relationship to cognitive concepts such as expectancy, competition, and resonance. The theory shows how a real-time analysis of an animal's adaptive behavior in prescribed environments can disclose network principles and mechanisms which imply a restructuring and unification of the data in terms of design principles and mechanisms rather than the vicissitudes of experimental methodology or historical accident. A comparative analysis and unification of other theories is then possible, such as the classical theories of Hull, Spence, Neal Miller, Estes, Logan, Livingston, and John. The data which are discussed include overshadowing and unblocking; suppression by punishment; reinforcement contrast effects; hypothalamic self-stimulation; differential effects of drive, reinforcement, incentive motivation, expectancies, and short-term memory competition on learning rate, behavioral choice, and performance speed; the role of polyvalent cortical cells, multiple sensory representations, recurrent on-center off-surround neocortical and paleocortical interactions, hippocampal-hypothalamic, medial forebrain bundle, and thalamocortical interactions on motivated behavior; effects of drugs like chlorpromazine, reserpine, monoamine oxidase inhibitors and amphetamine on instrumental behavior. Of special interest are network 'hippocampal' computations that are suggested to accomplish several distinct roles: influence transfer of short-term to long-term memory both directly and indirectly, directly by triggering conditioning of conditioned reinforcers, indirectly by generating positive attentional feedback to neocortical polyvalent cells; and influence the organization of a motor map which controls approach and avoidance behavior by eliciting motivationally biased signals to this motor mapping system.

# **Some Psychophysiological and Pharmacological Correlates of a Developmental, Cognitive and Motivational Theory<sup>a</sup>**

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**PART I**

**1. INTRODUCTION: SELF-ORGANIZING INTERNAL REPRESENTATIONS**

Studies of event-related potentials (ERPs) can probe a level of neural organization that has behavioral meaning. ERP experiments thereby encourage us to formulate precisely the design problems that are solved by the behaving brain and to translate these design statements into a formal language that is powerful enough to explain how behavioral, physiological, and pharmacological processes are related.

I suggest that these design problems have eluded traditional physical and mathematical thinking because they address a fundamentally new physical situation. These problems concern the design of self-organizing systems, or systems that can generate new internal representations in response to changing environmental rules. This article sketches a psychophysiological theory of how new internal representations are generated. The theory suggests how some ERP-creating mechanisms help to control the self-organization process and how to test these assertions empirically.

In particular, I will suggest that a P300 can be elicited whenever short term memory (STM) is reset by a massive antagonistic rebound within the catecholamine arousal system (Grossberg, 1972b; 1976b; 1978a; 1980a). This suggestion illustrates a sense in which P300s with different anatomical generators can be functionally similar. It also shows why task relevance is important in eliciting P300s, since STM cannot be reset unless it is already active. I will also indicate, however, how a neocortical rebound might elicit a hippocampal rebound by rapidly inhibiting reinforcing signals from cortex to hippocampus. Since the cortical rebound resets a cognitive process and the hippocampal rebound resets a motivational process in the theory (Grossberg, 1975), P300s with different anatomical generators can be functionally dissimilar. Due to the importance of interactions between cognitive and motivational processes for the understanding of both types of processes, I will discuss both cognitive and motivational processes herein and will suggest new explanations and predictions in both domains using the same mechanisms, albeit in different anatomical configurations. I will also suggest that functional homologues of many normal and abnormal motivational properties exist in cognitive properties due to the control of both classes of properties by common mechanisms, notably mechanisms mediated by cholinergic-catecholaminergic interactions. Using these homologues, known motivational phenomena can be used to suggest designs for new types of cognitive experiments and *vice versa*.

The theory also suggests how a mismatch detector, which regulates mismatch negativity in the theory, can sometimes elicit a P300 by triggering a burst of nonspecific arousal to the catecholamine system. An unexpected event can thereby elicit a formal N200 followed by a P300.



## 7. Biological Rhythms and Mental Disorders

Articles: 2, 3, 4, 5, 21.

This work represents a major development of the theory of gated dipoles. This is a neural theory of opponent processing which has been of as much use in our work on color theory (characterizing double opponent red-green or blue-yellow cortical cells) as it has been in our analyses of cognitive self-organization (reset of attentional focus by an unexpected event) or of reinforcement and motivation (characterizing interactions between fear-relief or hunger-frustration) in midbrain reinforcement circuits. Thus the gated dipole opponent process design appears to be ubiquitous in the nervous system.

The present work develops a class of gated dipole properties which are important in all these areas: their ability to generate endogenous rhythms. Such rhythms, with variable frequencies, occur in a number of different neural systems. In particular, we have discovered how a gated dipole circuit can generate endogenous rhythms whose free-running period can be tuned by a single network parameter. In the present work, we have exploited a large quantitative data base about circadian rhythms to develop gated dipole designs of endogenous oscillators. Such rhythms are of independent interest to AFOSR because of their role in contributing to jet lag and to other performance decrements which arise from interactions between activity and light cycles.

Our first discovery was of a specialized gated dipole circuit that behaves like a circadian pacemaker. Using this insight, a theory of circadian rhythms was developed and used to quantitatively simulate a large data base concerning the rhythmic behaviors controlled by the mammalian suprachiasmatic nuclei of the hypothalamus. The appetitive hypothalamic circuits of the theory (eating, drinking, sex, fear) are also built up from gated dipole components. Thus the theory suggests that several functionally distinct hypothalamic circuits are synthesized from gated dipole components.

The theory indicates how the circadian pacemaker can modulate the sensitivity of

appetitive and cognitive circuits, and analyses how ultradian (several hour) appetitive cycles (e.g., eating) are superimposed upon circadian cycles. These circadian and ultradian modulatory circuits help to regulate how attentional resources are reallocated to different classes of sensory and cognitive cues due to the shifting balance of motivational factors through time. It is shown how a breakdown in the relationship between these circuits can lead to symptoms characteristic of certain mental disorders: e.g., juvenile hyperactivity and simple schizophrenia. These results have opened the path to discovery of the auxiliary mechanisms whereby such circuits can automatically tune their own parameters to remain within an optimal operating range.

Abstracts of two articles are included below

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## **A Neural Theory of Circadian Rhythms: The Gated Pacemaker**

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**Abstract.** This article describes a behaviorally, physiologically, and anatomically predictive model of how circadian rhythms are generated by each suprachiasmatic nucleus (SCN) of the mammalian hypothalamus. This gated pacemaker model is defined in terms of competing on-cell off-cell populations whose positive feedback signals are gated by slowly accumulating chemical transmitter substances. These components have also been used to model other hypothalamic circuits, notably the eating circuit. A parametric analysis of the types of oscillations supported by the model is presented. The complementary reactions to light of diurnal and nocturnal mammals as well as their similar phase response curves are obtained. The "dead zone" of the phase response curve during the subjective day of a nocturnal rodent is also explained. Oscillations are suppressed by high intensities of steady light. Operations that alter the parameters of the model transmitters can phase shift or otherwise change its circadian oscillation. Effects of ablation and hormones on model oscillations are summarized. Observed oscillations include regular periodic solutions, periodic plateau solutions, rippled plateau solutions, period doubling solutions, slow modulation of oscillations over a period of months, and repeating sequences of oscillation clusters. The model period increases inversely with the transmitter accumulation rate but is insensitive to other parameter choices except near the breakdown of oscillations. The model's clocklike nature is thus a mathematical property rather than a

formal postulate. A singular perturbation approach to the model's analysis is described.

# A neural theory of circadian rhythms: Aschoff's rule in diurnal and nocturnal mammals

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CARPENTER, GAIL A., AND STEPHEN GROSSBERG. A neural theory of circadian rhythms: Aschoff's rule in diurnal and nocturnal mammals. *Am. J. Physiol.* 247 (Regulatory Integrative Comp. Physiol. 16): R1067-R1082, 1984.—A neural model of the suprachiasmatic nuclei suggests how behavioral activity, rest, and circadian period depend on light intensity in diurnal and nocturnal mammals. These properties are traced to the action of light input (external zeitgeber) and an activity-mediated fatigue signal (internal zeitgeber) on the circadian pacemaker. Light enhances activity of the diurnal model and suppresses activity of the nocturnal model. Fatigue suppresses activity in both diurnal and nocturnal models. The asymmetrical action of light and fatigue in diurnal vs. nocturnal models explains the more consistent adherence of nocturnal mammals to Aschoff's rule, the consistent adherence of both diurnal and nocturnal mammals to the circadian rule, and the tendency of nocturnal mammals to lose circadian rhythmicity at lower light levels than diurnal mammals. The fatigue signal is related to the sleep process S of Borbély (*Hum. Neurobiol.* 1: 195-204, 1982.) and contributes to the stability of circadian period. Two predictions follow: diurnal mammals obey Aschoff's rule less consistently during a self-selected light-dark cycle than in constant light, and if light level is increased enough during sleep in diurnal mammals to compensate for eye closure, then Aschoff's rule will hold more consistently. The results are compared with those of Enright's model.

hypothalamus; suprachiasmatic nuclei; transmitter gate; instrumental behavior

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